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Dynamic integration of information about salience and value for smooth pursuit eye movements

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ABSTRACT

Eye movement behavior can be determined by bottom-up factors like visual salience and by top-down factors like expected value. These different types of signals have to be combined for the control of eye movements. In this study we investigated how smooth pursuit eye movements integrate salience and value information. Observers were asked to track a random-dot kinematogram containing two coherent motion directions. To manipulate salience, the coherence or the density of one of the motion signals was varied. To manipulate value, observers won or lost money in a separate experiment if they were tracking one or the other motion direction. Our results show that pursuit direction was initially determined only by salience. 300–400 ms after target motion onset, pursuit steered towards the rewarded direction and the salience effects disappeared. The time course of this effect depended crucially on the difficulty to segment the two signal directions. These results indicate that salience determines early pursuit responses in the same way as saccades with short latencies. Value information is processed slower and dominates pursuit after several 100 ms.

1. Introduction

Humans use saccadic eye movements to foveate objects of interest and smooth pursuit eye movements to stabilize moving objects on the fovea. Of course, natural environments contain several targets at the same time, so that selection is an integral purpose of eye movements. Target selection for saccades has been studied intensively and a variety of different signals that can guide saccades have been identified (Schütz, Braun, & Gegenfurtner, 2011): Amongst others, saccades are executed towards salient image locations (Itti & Koch, 2000; Kienzle et al., 2009), towards objects (Einhäuser, Spain, & Perona, 2008; Nuthmann & Henderson, 2010), towards locations that maximize the expected value (Schütz, Trommershäuser, & Gegenfurtner, 2012) and are also controlled by current action planning (Ballard, Hayhoe, & Pelz, 1995; Johansson et al., 2001). The integration of these different types of signals is further complicated by the different time course of each of these signals. Recently we showed that salience and value information receive different relative weights depending on the saccade latency: saccades with latencies shorter than 180 ms favor salience, whereas saccades with latencies longer than 180 ms favor value (Markowitz et al., 2011; Schütz, Trommershäuser, & Gegenfurtner, 2012).

Compared to saccades, signals that affect smooth pursuit target selection are less well studied. In general, smooth pursuit can only be executed with a high gain in response to visual motion (Berryhill, Chiu, & Hughes, 2006). In the presence of two moving targets, the initial pursuit response is typically a vector average of both motion directions (Lisberger & Ferrera, 1997). Similar to saccades, smooth pursuit prefers stimuli with higher salience, such as higher contrast (Liston & Krauzlis, 2003) or stronger motion energy (Krauzlis & Adler, 2001; Schütz, 2011). Interestingly, smooth pursuit shows a stronger preference for luminance contrast compared to color contrast than saccades (Spering, Montagnini, & Gegenfurtner, 2008), which means that salience processing might not be identical for different types of eye movements. Besides low-level motion processing factors, there are also high-level factors influencing pursuit. Predictive onset and direction of motion can lead to anticipatory pursuit (Kowler, 1989). Similar to saccades, instructions and reward can bias the target selection for smooth pursuit. When two targets differ in their reward and a cue informs about the motion direction of the two targets, pursuit initiation is biased towards the rewarded motion direction (Ferrera, 2000; Joshua & Lisberger, 2012). Non-visual feedback can also increase pursuit gain during transient target blanking (Madelain & Krauzlis, 2003). A still remaining question

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is how different types of signals are traded off in the control of pursuit movements. For instance in a landscape one might encounter two flying birds, a duck and a kingfisher. The duck is certainly more salient because of its size, whereas the kingfisher might be more valuable to look at, because of its beauty. The brain has to resolve this conflict and select one of the two birds for pursuit. A previous study showed that top-down knowledge about the two-dimensional motion direction of a tilted bar does not allow to compensate for the biased one-dimensional edge motion (Montagnini, Spering, & Masson, 2006). This finding suggests that bottom-up stimulus information can even override top-down expectations.

Here we investigated how salience and value information are traded off in the control of smooth pursuit eye movements. Smooth pursuit eye movements are especially interesting in this respect, because each single smooth pursuit trace provides a continuous read-out of this integration process. The previous results on saccades (Schütz, Trommershäuser, & Gegenfurtner, 2012) suggest that the relative weighting of salience and value is not constant, but changes over time.

2. Methods

2.1. Subjects

The author FL and seven naïve observers participated in these experiments. Six observers participated in the first experiment; three observers participated in the second experiment. We had to exclude the data of one observer in the first experiment, because she/he was not able to segment the two motion directions at all. Experiments were in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and approved by the local ethics committee LEK FB06 at the University Giessen (proposal number 2009-0008). Written informed consent was obtained from all observers.

2.2. Equipment

Observers were seated in a dark room facing a 21-in. SONY GDM-F520 CRT monitor driven by an Nvidia Quadro NVS 290 graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45 degrees of visual angle in the horizontal direction, and 36 degrees of visual angle vertical on the subject's retina. With a spatial resolution of 1280 × 1024 pixels this results in 28 pixels/degrees of visual angle. The observers's head was stabilized by a chin and a forehead rest and the display was viewed binocularly. Eye position signals of the right eye were recorded with a video-based eye tracker (EyeLink 1000; SR Research Ltd., Kanata, Ontario, Canada) and were sampled at 1000 Hz. Stimulus display and data collection were controlled by a PC.

2.3. Visual stimuli

All stimuli were presented on a gray background with a luminance of 14.6 cd/m^2. Two random dot kinematograms (RDKs) appeared within a circular aperture of 20 degrees of visual angle radius. This aperture was slightly cropped at the bottom and top because the height of the monitor was only 36 degrees of visual angle. Individual dots were displayed in white (87 cd/m^2) or black (0.04 cd/m^2) and had a size of 0.14 × 0.14 degrees of visual angle. The dots had a life time of 200 ms and at the end of their life time they were positioned at a random position in the aperture. Each dot kept its motion direction for the whole 200 ms, such that signal dots could be segmented from noise dots, leading to the appearance of transparent motion (Schütz et al., 2010). The motion speed was 10 degrees of visual angle/s. The overall motion direction was either leftward or rightward with the motion directions of the two RDKs deflected upward or downward from horizontal by 10°. We used RDKs with a limited dot-lifetime to study smooth pursuit in isolation without intervening saccades. Although saccades and smooth pursuit typically share a common target selection mechanism (Case & Ferrera, 2007; Krauzlis, Dill, & Fowler, 2012), they differ in salience computations (Spering, Montagnini, & Gegenfurtner, 2008) and also might differ in reward processing. We could show that a RDK elicits only few saccades (Schütz et al., 2010).

2.4. Experimental procedure

At the beginning of each trial a bull's eye with an outer radius of 0.3 degrees of visual angle and an inner radius of 0.075 degrees of visual angle appeared at the screen center. The observers had to fixate the bull's eye and press a button to start the trial, at which time the EyeLink 1000 System performed a fixation check. If the fixation check succeeded, the initial bull's eye disappeared and the random-dot kinematogram appeared. Motion started as soon as the dots appeared. The random-dot kinematogram was presented for 2000 ms (Fig. 1A).

2.5. Salience and value conditions

Observers participated in two different conditions: in the salience condition, there was no reward or penalty. The salience condition also consisted of single-target trials with only one RDK to measure the variability of smooth pursuit direction in the absence of a target conflict. In the value condition, observers could win up to 100 points per trial if they followed the white RDK and could lose up to 100 points if they followed the black RDK. After each trial we calculated the eye movement direction in a time window from 150 to 1500 ms after target motion onset. If the eye movement direction was within 10° of the direction of the white RDK in the whole time window, the observers won 100 points for one trial. If the eye movement direction was within 10° of the direction of the black RDK during the whole time window, the observers lost 100 points. The points in one trial were calculated according to the proportion of time that the eyes were moving in the rewarded or punished direction. The points earned during the trial and the total sum of points was displayed after each trial. Points were transformed into money at the end of the experiment, such that observers could maximally win 3 € in addition to the regular compensation of 8 € per hour.

2.6. Eye movement analysis

Eye velocity signals were obtained by digital differentiation of eye position signals over time. The eye position and velocity signals were filtered by a Butterworth filter with cut-off frequencies of 30 and 20 Hz, respectively. Saccade onset and offset were determined with the EyeLink saccade algorithm. This algorithm uses a velocity threshold of 22 degrees of visual angle/s to which the average velocity over the last 40 ms is added and an acceleration threshold of 3800 degrees of visual angle/s^2. Saccades were removed from the velocity traces by linear interpolation. All traces were rotated such that the overall target motion was to the right and the motion of the white and black RDK was upwards and downwards, respectively. Since left and right motion and up- and downward motion were balanced, any potential bias towards one of these directions cannot contaminate our results. We also did not observe any systematic direction biases in single-target trials. For each trace, the angular direction of the eye velocity was calculated in 100 ms wide time intervals, starting 200 or 900 ms after target motion onset. We only analyzed directions within −25° to 25°. Circular statistics

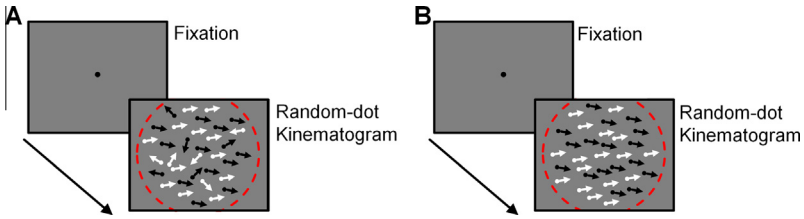

Fig. 1. Experimental paradigm. (A) Experiment 1. Salience was manipulated by changing the coherence of the black RDK. (B) Experiment 2. Salience was manipulated by changing the density of the black RDK. (A) and (B) The red line indicates the invisible border of the aperture.

were calculated using the circular statistics toolbox (Berens, 2009). Smooth pursuit latency was analyzed using a two-step procedure (Schütz et al., 2010). First, the latency of average smooth pursuit traces was determined as the zero-crossing of the best-fitting regression on eye velocity (Schütz, Braun, & Gegenfurtner, 2007). Second, the latency of individual traces was estimated by shifting each individual trace on the time axis such that the deviation to the average trace was minimized (Osborne, Lisberger, & Bialek, 2005).

2.7. Experiments

We performed two different experiments, in which we used two ways to manipulate the relative salience of the two motion directions. In the first experiment, both RDKs had a dot density of 0.5 dots/degrees^2 of visual angle (628 dots) and the coherence of the RDKs was varied. The white RDK had a fixed coherence of 40% and the black RDK had coherences of 20%, 40% or 80%. In the second experiment, both RDKs were 100% coherent and the dot density of the RDKs was varied (Schütz, 2011). The white RDK had a dot density of 0.2 dots/degrees of visual angle^2 (251 dots) and the black RDK had a dot density of 0.1 (126), 0.2 (251) or 0.4 dots/degrees of visual angle^2 (503 dots). Since we merely wanted to test an alternative way to manipulate salience, we do not distinguish between dot density or dot number in the second experiment.

2.8. Modeling

We used a modified version of a model that has been used previously to account for the integration of salience and value for saccades (Schütz, Trommershäuser, & Gegenfurtner, 2012). In this model, the average smooth pursuit direction in the salience condition (θ_s), and the motion direction of the rewarded RDK (θ_r) are combined using the relative weights (w), in order to predict smooth pursuit direction of single traces in the value condition (θ_v):

$$\theta_v(t,\mu,\sigma,w_{\max}) = \theta_s(1 - w(t,\mu,\sigma,w_{\max})) + \theta_r w(t,\mu,\sigma,w_{\max}) \quad (1)$$

The relative weights (w) of salience and value are determined as a function of time (t), using a cumulative Gaussian function with the free parameters standard deviation (σ), the point of equal weight of salience and value (μ), and the maximum value weight ($w_{\max}$):

$$w(t,\mu,\sigma,w_{\max}) = w_{max}\frac{1}{\sigma\sqrt{2\pi}}\int_{T>-\infty}^{T<t} e^{\frac{-(T-\mu)^2}{2\sigma^2}}dT \quad (2)$$

In total the model contains three free parameters: μ_t (mean), σ_t (standard deviation) and $w_{\max}$ (maximum value weight) for the latency dependent weighting of visual salience and value. The model was fitted to each trace in the value condition. We only included traces with positive correlation between predictions from the model and the data (87 ± 4% and 85 ± 8% in the coherence and density experiment, respectively).

3. Results

3.1. Experiment 1: Motion coherence

We measured the influence of salience in isolation when observers were tracking the motion without any specific instructions about reward or penalty. To manipulate salience, we varied the motion coherence of the black RDK (Fig. 2A and D). The eye velocity increased about 100 ms after the target motion onset and reached a constant value 500 ms after target motion onset. The initial acceleration of pursuit was positively related to the coherence of the black RDK, such that higher coherences led to faster acceleration. In a previous study we observed a similar influence of coherence with only one coherent signal (Schütz et al., 2010).

The initial eye direction was also affected by the coherence of the black RDK. Consistently with a vector average prediction (Lisberger & Ferrera, 1997), the initial eye direction was biased towards the RDK with higher coherence. In addition to this vector average effect, the eye direction was biased towards the black RDK, which could be caused by a salience advantage of dark over bright regions (Komban, Alonso, & Zaidi, 2011; Lu & Sperling, 2012), presumably due to an excess of OFF cells (Ratliff et al., 2010). Consistent with this finding, saccades are also more strongly attracted by dark spots compared to bright spots (Rasche & Gegenfurtner, 2010). In a control condition with only one coherent signal, the eye direction was close to the target motion direction from about 200 ms.

Of course the average eye movement traces do not allow to differentiate between a true vector average in single trials or a winner-take-all in single trials with different winners in different trials. To analyze the eye movement direction more closely on a single trial basis, we calculated the average eye direction in time intervals from 200 to 300 ms and 900 to 1000 ms after target motion onset (Figs. 3A and C and 4A, C and E; Movie 1). The early time window should reflect the initial pursuit direction whereas the late time window should reflect the final target selection. The mean of the distributions differed between the three coherence conditions ($F(2,8) = 125.71$, $P < 0.001$) and there was also a significant interaction between coherence and time window ($F(2,8) = 15.89$, $P = 0.001$). Eye movement directions during the initiation peaked between the motion directions of the two RDKs and were offset according to the coherence level of the black RDK. Since each of the distributions had only a single peak, initial pursuit actually integrated both motion directions. In the steady-state phase, pursuit showed mainly a winner-take-all behavior, such that eye movement directions peaked close to one of the directions of the two RDKs. As an exception from this general pattern, the distributions of one observer were quite broad. Since the distributions neither peaked at the vector average, nor showed a clear bimodal structure with peaks at the individual motion directions, this observer seemed to use both, vector-average and winner-take-all strategies in different trials (Fig. 4A).

In a second condition, we instructed observers that they gain money if they follow the white RDK and that they lose money if

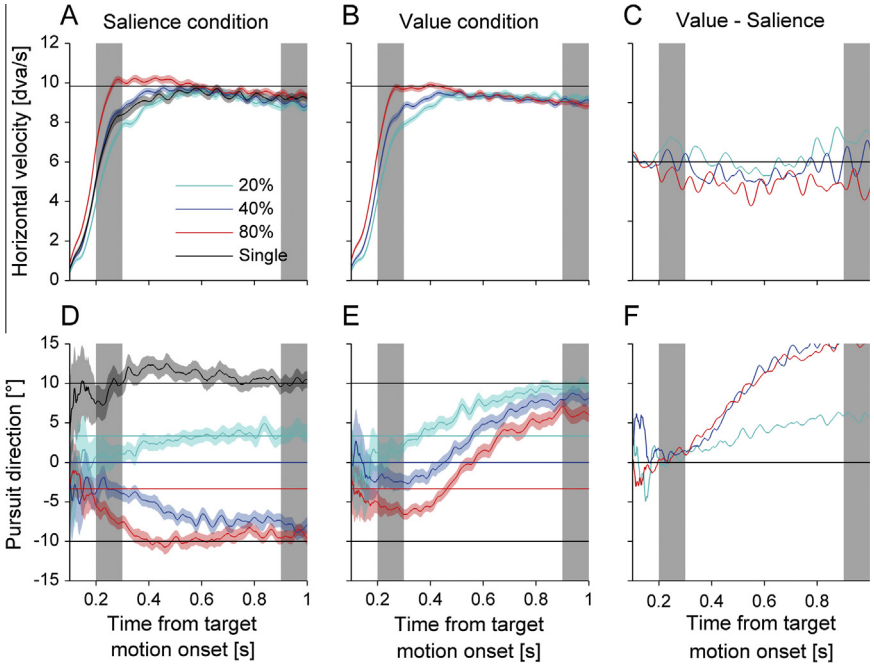

Fig. 2. Smooth pursuit eye movement traces in the coherence experiment. (A)–(C) Average horizontal smooth pursuit eye velocity over time across five observers. (D)–(F) Average smooth pursuit eye direction over time across five observers. The black horizontal lines indicate the motion directions of the white (fixed coherence 40%, 10°) and the black RDK (variable coherence, −10°). The colored horizontal lines indicate the vector average predictions for the different coherence conditions. (A) and (D) Salience condition. (B) and (E) Value condition. Here the white RDK is associated with a reward and the black RDK associated with a penalty. (C) and (F) Difference between value and salience condition. (A)–(F) The three different colors indicate the three different coherence levels. The black trace indicates the single target condition. Shaded areas represent 95% confidence intervals. The gray shaded areas mark the time windows in which the direction distributions were measured (Fig. 3).

they follow the black RDK (Fig. 2B and E). The horizontal eye velocity and acceleration were very similar as in the salience condition. Initial eye direction was also very similar to the salience condition as it was biased towards the more coherent RDK as expected from a vector average. However, about 300 ms after target motion onset, the eyes steered towards the rewarded RDK, reflecting an influence of value (Fig. 2F). At the same time, the difference between the different coherence conditions became smaller, indicating that the influence of salience decreased. The analysis of eye direction in the two analysis intervals revealed significant effects of coherence ($F(2,8) = 45.78$, $P < 0.001$) and of time window ($F(1,4) = 55.66$, $P = 0.002$) and a significant interaction ($F(2,8) = 7.34$, $P = 0.016$). 200–300 ms after target motion onset, eye movement directions peaked in between the two motion directions, with a bias towards the more coherent motion direction. 900–1000 ms after target motion onset, eye movement directions peaked at the motion direction of the rewarded RDK, for all three coherence conditions (Figs. 3B and D and 4B, D and F; Movie 1). This qualitative difference to the salience condition was supported by a significant interaction between condition (salience versus value) and time window ($F(2,4) = 67.44$, $P = 0.001$). Interestingly the distributions in the value condition were positively skewed in the late time window. This suggests that the observers could not suppress the distracting motion direction completely in all trials.

The slow transition from salience to value, evident in the average traces (Fig. 2E), could be caused by a slow transition on a single trial basis or by fast transitions in single trials that occur at different points in time. Even the analysis of the distribution of eye movement directions does not distinguish well between these alternatives. In order to capture the relative weighting of salience and value information and its timing more precisely, we fitted a model that has been used previously for saccadic eye movements (Schütz, Trommershäuser, & Gegenfurtner, 2012). In this model, the relative weighting of predictions based on salience and value was modeled by a cumulative Gaussian function (Fig. 5A and C). The average eye movement traces from the salience condition were used as the salience prediction. For the value prediction we did not calculate the optimal pursuit direction as in the original MEGaMoveModel (Trommershäuser, Maloney, & Landy, 2003), because smooth pursuit eye movements can be executed only in motion directions that are actually present in the visual display. Hence we used the motion direction of the rewarded RDK as the value prediction. This assumption might over-estimate the value weight, if the optimal pursuit direction is more eccentric than the motion direction of the rewarded RDK. The model contains three free parameters: the mean and standard deviation of the cumulative Gaussian function and the maximal asymptotic weight that is assigned to value (Eqs. (1) and (2)). The model was fitted to each eye movement trace in the value condition.

The transition parameters between salience and value were a mean of 419 ± 31 ms (Fig. 6A) and a standard deviation of 118 ± 24 ms (Fig. 6C). This means that the weight assigned to value exceeded the weight assigned to salience after about 419 ms. Relative to the pursuit latency of 106 ± 52 ms, this is a delay of 313 ms. The distribution of parameters shows that the transition time varied between trials substantially for two observers. This suggests that the slow transition from salience to value is partially caused by variations in the onset of the transition across different trials. Nevertheless, compared to saccadic eye movements, where the transition between salience and value occurs around 180 ms and took about 30 ms (Schütz, Trommershäuser, & Gegenfurtner, 2012), the transition between salience and value occurred rather late and was slower for smooth pursuit eye movements (Fig. 5C). Besides the transition between salience-dominated and value-dominated behavior, it is interesting to look at the earliest effect of value. This time can be estimated as the point in time when the value weight reached a threshold of 10%, which happened at 269 ± 16 ms and 162 ± 23 ms after target or pursuit onset

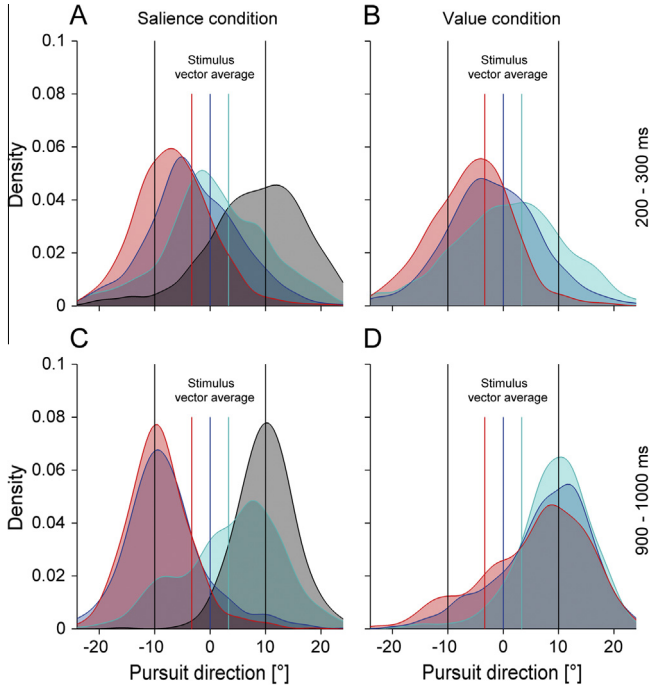

Fig. 3. Distributions of smooth pursuit eye movement directions in the coherence experiment. (A) and (B) Pursuit direction distributions in the early time window 200–300 ms after target motion onset. (C) and (D) Pursuit direction distributions in the late time window 900–1000 ms after target motion onset. (A) and (C) Salience condition. (B) and (D) Value condition. (A)–(D) The black vertical lines indicate the motion directions of the white (fixed coherence 40%, 10°) and the black RDK (variable coherence, −10°). The colored vertical lines indicate the vector average predictions for the different coherence conditions. Distributions show probability density with a Gaussian distribution with a standard deviation of 2°.

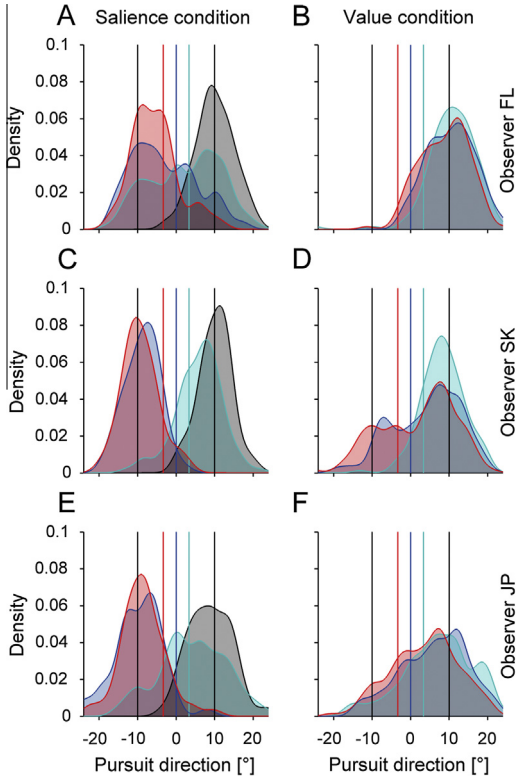

Fig. 4. Distributions of smooth pursuit eye movement direction in the coherence experiment for three observers in the late time window 900–1000 ms after target motion onset. (A), (C) and (E) Salience condition. (B), (D) and (F) Value condition. (A) and (B) Observer FL. (C) and (D) Observer SK. (E) and (F) Observer JP. (A)–(F) Conventions are the same as in Fig. 3.

respectively. These values are similar to the duration of the open-loop period, before feedback from the eyes becomes available.

The maximum value weight was 86 ± 7% (Fig. 6E), which means that smooth pursuit was not exclusively following the rewarded motion direction, even at late time intervals. Of course it might be possible that observers would be able to maximize their reward even by pursuing an intermediate direction. To rule out this possibility, we calculated for each observer separately the optimal direction that maximizes reward based on the individual variability in eye movement direction with a single RDK. This direction was very close to the rewarded direction and only offset by 0.74 ± 0.24°, away from the penalized direction. Hence the maximum value weight calculated relative to the optimal pursuit direction, rather than relative to the rewarded pursuit direction, would be even slightly lower.

3.2. Experiment 2: Density/dot number

In the second experiment, we used 100% coherent RDKs and manipulated salience by varying the density in the black RDK. Since there were no noise dots, this condition should facilitate the segmentation of the two RDKs and the identification of the rewarded motion direction. This should be reflected in a faster transition from salience to value and a larger maximum weight that is assigned to value.

The horizontal eye velocity and acceleration were not affected by the density in the black RDK in the salience condition (Fig. 7A and D), suggesting that the general initiation of smooth pursuit was not affected by the RDK density. However the density affected the direction of smooth pursuit eye movements. Pursuit direction was biased towards the RDK with higher density (Schütz, 2011),

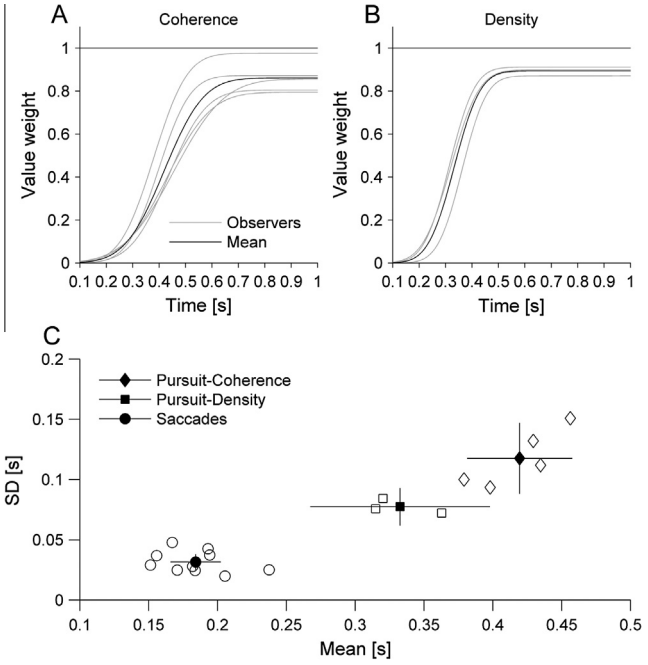

Fig. 5. Modelling results. (A) and (B) Value weights over time from target motion onset. The gray lines represent individual observers; the black line the average across observers. Value weights are expressed by cumulative Gaussian functions. (A) Coherence experiment. (B) Density experiment. (C) Mean and standard deviation of the value weight functions. The saccade data are taken from Schütz, Trommershäuser, and Gegenfurtner (2012).

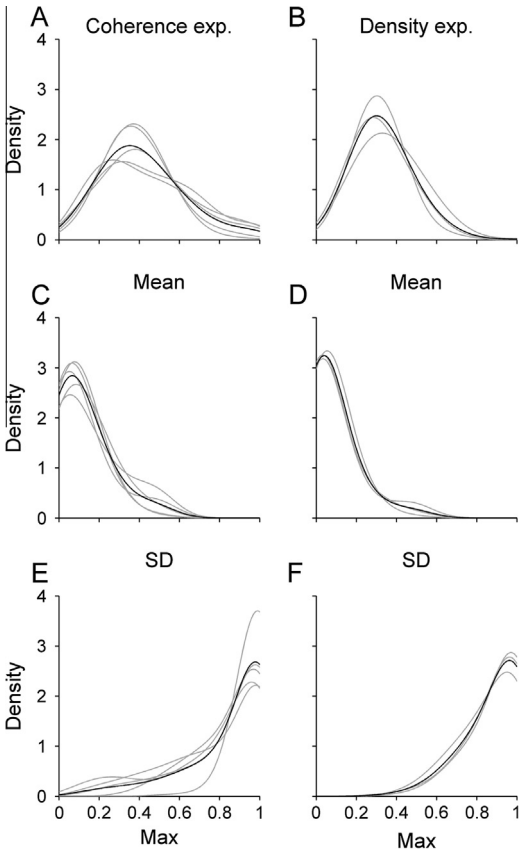

Fig. 6. Modelling, distribution of fitted parameters. (A) and (B) Mean of the cumulative Gaussian function. (C) and (D) Standard deviation of the cumulative Gaussian function. (E) and (F) Maximum reward weight. (A), (C) and (E) Coherence experiment. (B), (D) and (F) Density experiment. (A)–(F) The gray lines represent individual observers; the black line the average across observers. Distributions show probability density with a Gaussian distribution with a standard deviation of 0.1.

which is consistent with a vector average computation and similar to the results of the coherence experiment. In contrast to the coherence experiment, this averaging behavior remained present throughout the whole trial. Indeed, eye movement directions were broadly distributed during the initiation and the steady-state phase of pursuit (Figs. 8A and C and 9A, C and E; Movie 2) and there was no effect of time window ($F(1,2) = 0.18$, $P = 0.712$). However there was a significant effect of density ($F(2,4) = 126.01$, $P < 0.001$), such that the distributions were biased towards the motion direction with higher density. In the late time window, the distributions of eye movement directions were broader in the conditions with two RDKs than in the control condition with only one RDK. Since the eye movement directions were broadly distributed in the late time window, and did neither peak at the vector average nor at the actual target directions, the observers seemed to use both vector average and winner-take-all strategies in different trials.

The results in the value condition (Fig. 7B and E) were very similar to the coherence experiment. The eyes initially followed a vector average direction and later steered towards the rewarded direction. At the same time the difference between the three density conditions was reduced, reflecting a reduced influence of visual salience. However the direction change towards the rewarded direction occurred much earlier, at about 250 ms after target motion onset (Fig. 7F). The analysis of eye movement directions revealed significant effects of density ($F(2,4) = 108.21$, $P < 0.001$), time window ($F(1,2) = 316.10$, $P = 0.003$) and a significant interaction ($F(2,4) = 28.01$, $P = 0.004$). 200–300 ms after target motion onset, eye movement directions were broadly distributed, with peaks in between the two motion directions. 900–1000 ms after target motion onset, the distributions of eye movement directions peaked close to the rewarded direction (Figs. 8B and D and 9B, D and F; Movie 2). This difference between the salience and the value condition was supported by a significant interaction between condition and time window ($F(1,2) = 188.68$, $P = 0.005$). In the late time window the width of the distributions was similar to the distribution in the control condition with only one RDK. This indicates that the observers consistently selected the rewarded RDK in the value condition and that the remaining variability in eye movement direction did not stem from instable target selection.

We also predicted the eye movements in the value condition based on a weighted combination of the eye movements in the salience condition and the rewarded target motion direction (Fig. 5B and C). The transition parameters between salience and value were a mean of 333 ± 26 ms (Fig. 6B) and a standard deviation of 77 ± 6 ms (Fig. 6D). Relative to the pursuit latency of 90 ± 11 ms, the transition between salience and value was delayed by 243 ms. The earliest influence of value, as measured by the time when the value weight reached a threshold of 10%, was evident at 233 ± 32 ms and 143 ± 42 ms after target and pursuit onset, respectively. The maximum value weight was 89 ± 2% (Fig. 6F). Presumably the easier segmentation of the two RDKs with noise allowed a faster processing of the value information.

4. Discussion

In two experiments we investigated the integration of salience and value information in the control of smooth pursuit eye movements. The results showed that pursuit was initially governed by salience information. 230–270 ms after target motion onset, pursuit direction was first influenced by value. Only after 300–400 ms, depending on the experiment, smooth pursuit put a larger weight on value than salience (Figs. 2 and 7). We predicted single traces in the value condition with a model that uses a relative weighting of average eye movement directions in the salience condition and the rewarded target motion direction (Figs. 5 and 6).

The initial eye movement directions in all conditions were close to the predictions based on a vector average of all motion directions in the stimulus. This is consistent with previous results showing that initial pursuit direction is best explained by a vector average computation (Lisberger & Ferrera, 1997). In the salience condition without value manipulation, some observers showed a winner-take-all behavior towards the end of the trials in the coherence experiment. The remaining observers showed broad direction distributions at the end of the trials, indicating a mixture of vector averaging and winner-take-all strategies. This is in contrast to previous studies using dots instead of RDKs as stimuli, where only winner-take-all strategies were observed (Lisberger & Ferrera, 1997). Possibly some observers integrated over both RDKs instead of segmenting them in the salience condition. The small direction difference of 20° between the two RDKs presumably facilitated integration versus segmentation. Hence target selection seems to be optional with such a stimulus, since winner-take-all behavior was clearly present in the value condition.

Previous studies on value-modulations of smooth pursuit showed that value information can bias the initial pursuit direction, when the rewarded direction is cued in advance (Joshua & Lisberger, 2012), or when spatially-defined targets were used (Ferrera, 2000). In our paradigm, the rewarded direction was not predictable which allowed us to directly compare the time course of salience and value effects. Similar to saccades, we found that the

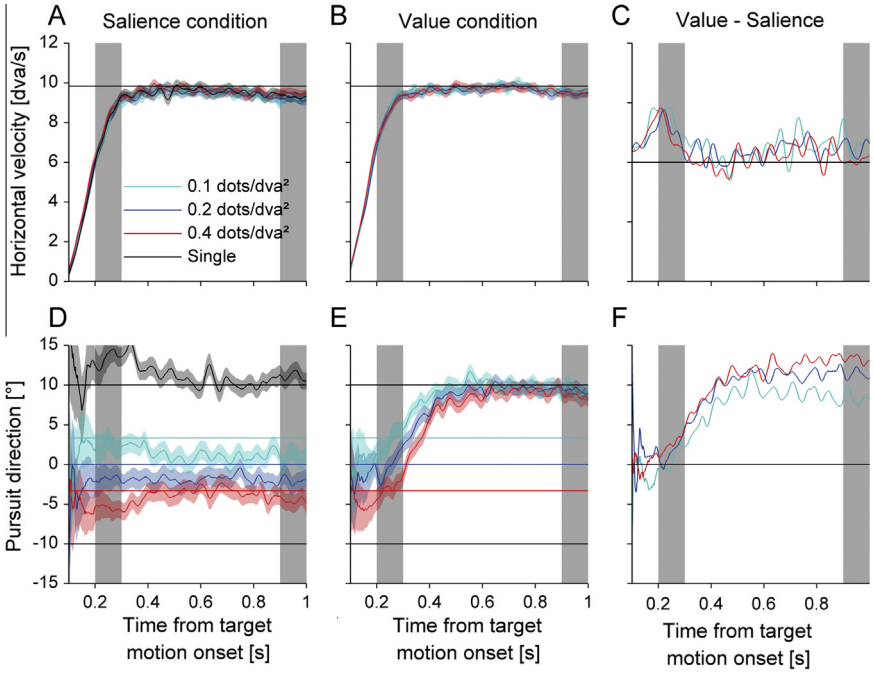

Fig. 7. Smooth pursuit eye movement traces in the density experiment. (A)–(C) Average horizontal smooth pursuit eye velocity over time across three observers. (D)–(F) Average of smooth pursuit eye direction over time across three observers. (A) and (D) Salience condition. (B) and (E) Value condition. Here the white RDK is associated with a reward and the black RDK associated with a penalty. (C) and (F) Difference between value and salience condition. (A)–(F) Conventions are the same as in Fig. 2.

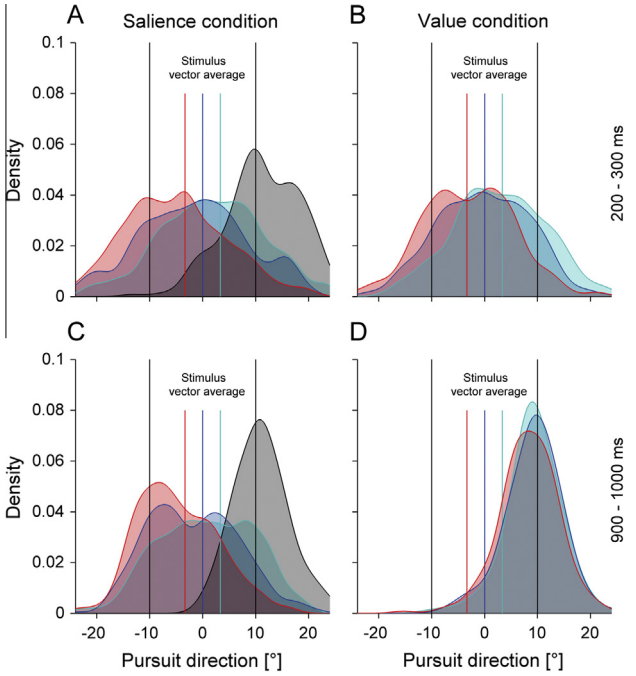

Fig. 8. Distributions of smooth pursuit eye movement directions in the density experiment. (A) and (B) Pursuit direction distributions in the early time window 200–300 ms after target motion onset. (C) and (D) Pursuit direction distributions in the late time window 900–1000 ms after target motion onset. (A) and (C) Salience condition. (B) and (D) Value condition. (A)–(D) Conventions are the same as in Fig. 3.

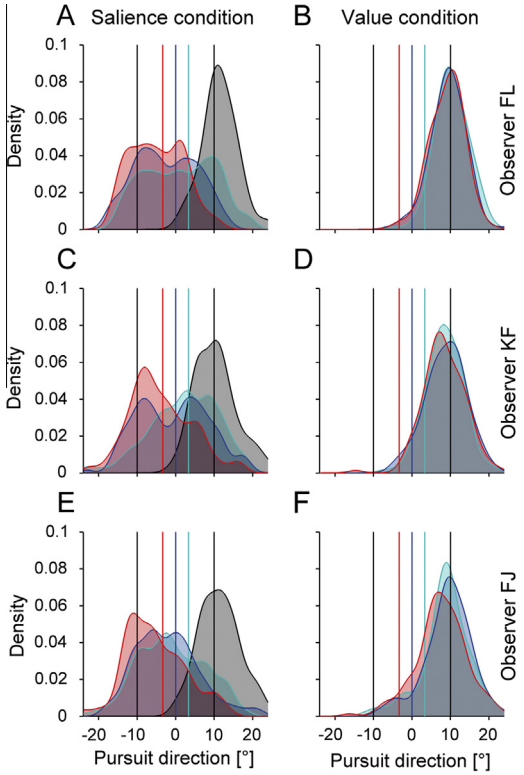

Fig. 9. Distributions of smooth pursuit eye movement direction in the density experiment for three observers in the late time window 900–1000 ms after target motion onset. (A), (C) and (E) Salience condition. (B), (D) and (F) Value condition. (A) and (B) Observer FL. (C) and (D) Observer KF. (E) and (F) Observer FJ. (A)–(F) Conventions are the same as in Fig. 3.

salience information dominates early eye movement behavior and value information only later on overrules salience. The first influence of value was detectable at 140–160 ms after pursuit onset or 230–270 ms after target motion onset. Subsequently, value received more and more weight until pursuit direction finally matched closely the rewarded motion direction. This onset of value-related eye movements coincides with the end of the open-loop period (Rasche & Gegenfurtner, 2009; Tychsen &

Lisberger, 1986). Possibly, the smooth pursuit system relies on visual feedback signals to fine-tune the pursuit direction to the rewarded motion direction.

A similar change in pursuit behavior has been observed in a number of different smooth pursuit paradigms. When two dots are moving in different directions, monkeys pursue a vector average of the two motion directions in the first 150 ms, before one of the two targets is selected and dominates the response (Ferrera, 2000; Lisberger & Ferrera, 1997). When tilted lines or diamonds are used as stimuli, the first 200 ms of pursuit follow the vector average of the stimuli, before the actual 2D motion direction is finally pursued (Masson & Stone, 2002; Wallace, Stone, & Masson, 2005). Furthermore it has been shown that the pursuit gain is enhanced by the execution of an initial catch-up saccade (Lisberger, 1998; Tanaka & Lisberger, 2001). This difference between pre- and post-saccadic pursuit has been linked to low- and high-level motion processing (Wilmer & Nakayama, 2007), suggesting different underlying motion mechanisms for pre- and post-saccadic pursuit.

4.1. Comparison with other types of movements

Qualitatively these results for smooth pursuit agree quite well with the results for saccadic eye movements (Schütz, Trommershäuser, & Gegenfurtner, 2012). Saccades with short latencies mainly follow salience and only saccades with long latencies are controlled such that they maximize the expected reward. For saccades, the gradual transition from salience to value was only visible across trials, for different saccades with different latencies. By measuring smooth pursuit eye movements in this study, it became evident that the gradual transition from salience to value also applies to single movements within one trial.

Quantitatively however, the transition between salience- and value-driven behavior occurred much later for smooth pursuit (300–400 ms after target motion onset) than for saccades (180 ms after target onset). This difference could either be caused by differences in the stimuli or reflect genuine differences between these eye movements. In both studies, reward and penalty were represented by opposite contrast polarities in the stimuli, but there are some fundamental differences. For saccades, only the location of darker and lighter areas had to be determined. For pursuit, the motion directions of two overlapping random-dot fields had to be segmented and reward and penalty had to be assigned. This segmentation might need more time than mere localization in the saccade-study. This is supported by our finding that the transition occurred earlier in the second experiment without direction noise. Moreover, the time course of the value influence on smooth pursuit was very similar to the time course of perception in an experiment where observers had to judge the depth ordering of comparable stimuli (Schütz, 2011). In this case, the eyes initially followed the motion direction with more dots and switched towards the motion direction that was perceptually relevant after 200–400 ms. Finally, not only the segmentation of the two surfaces might add a delay, but also the selection of the rewarded surface might be difficult. Even when two transparent motion surfaces are already segmented, it can take up to 600 ms to shift attention from one surface to a stimulus event on another surface (Valdes-Sosa, Cobo, & Pinilla, 2000).

Alternatively the delayed influence of value on smooth pursuit compared to saccades could reflect a genuine difference between pursuit and saccades. In the saccade study the latency effect was based on different trials with different saccades that were more or less controlled by salience or value. In the present study, the selected target and the tracked direction gradually changed over time during each smooth pursuit trace. Changing the direction of an ongoing pursuit movement might be more sluggish than changing the direction of a saccade during the preparation, before its actual execution. However saccade trajectories were curved, indicating also a dynamic influence of value for saccadic eye movements (Schütz, Trommershäuser, & Gegenfurtner, 2012). Previous studies about the competition of salience and value information for reaching movements found no effect of latency or salience on movement endpoints, suggesting that only value information guides the reaching movements (Trommershauser, Maloney, & Landy, 2003; Trommershäuser, Maloney, & Landy, 2003). A recent study however revealed that initial reach trajectories are also directed towards salient objects, before trajectories bend towards the actual target object (Wood et al., 2011). This indicates that different motor systems such as eye or hand movements as well as different movement types such as saccades and pursuit show a similar dynamic transition from bottom-up to top-down processing.

Another interesting quantitative difference between saccades and smooth pursuit in the two experiments is the maximum weight that is assigned to value information. Saccades are optimal after about 300–400 ms (Schütz, Trommershäuser, & Gegenfurtner, 2012), meaning that value information receives a weight of 100%. The maximum value weight for smooth pursuit was on average 86% in the coherence experiment and 89% in the density experiment. The lower value weight in the coherence experiment – and for pursuit in general – indicates that observers were not able to completely suppress the penalized motion direction in all trials. This is also apparent in the skewed distributions of eye movement directions in the value condition in this experiment (Fig. 3D).

4.2. Effects of reward with single targets

The current study investigated how salience and value affect smooth pursuit when two motion signals compete with each other. Thus it is concerned with target selection and the resulting eye movement control. Reward has previously been shown to affect the dynamics of eye movements when there is only a single target present. In this case, reward decreases smooth pursuit latency and increases acceleration slightly. These effects seem to be small in magnitude, compared to the effects on target selection (Joshua & Lisberger, 2012). Similar to pursuit, reward also leads to a decrease in saccade latency (Milstein & Dorris, 2007; Rothkirch et al., 2013; Takikawa et al., 2002) and an increase in saccade peak velocity (Chen et al., 2013; Takikawa et al., 2002; Xu-Wilson, Zee, & Shadmehr, 2009). The mechanisms underlying these effects of reward on the dynamics of eye movements were probably also at work in our paradigm. However since our value condition combined reward and penalty at the same time, these mechanisms potentially canceled each other out.

4.3. Neurophysiological basis

By comparing target competition in smooth pursuit for overlapping and non-overlapping targets, Niu and Lisberger (2011) reasoned that there must be two different stages for target competition: one at sensory processing for overlapping targets and one at later sensory-motor processing for non-overlapping targets. In our case, with two overlapping RDKs, the initial competition presumably took place at the sensory processing stage. The middle-temporal area contains direction selective neurons (Albright, 1984), which are causally involved in smooth pursuit initiation (Newsome et al., 1985). Hence the initial salience-driven pursuit responses in our paradigm could result from competition in area MT. Possible candidates for competition at a later stage, are the frontal eye fields (FEF), the lateral intraparietal area (LIP) and the superior colliculus (SC) (Krauzlis, 2004). Areas in the parietal cortex, which are involved in the control of eye movements

were amongst the first that have been explored for value processing. Several studies have provided evidence that activity in the LIP area (Platt & Glimcher, 1999; Sugrue, Corrado, & Newsome, 2004) and the SC (Ikeda & Hikosaka, 2003) is modulated by expected value. In the following, reward-related signals have been identified also in the visual cortex, including the primary visual cortex V1 (Serences, 2008; Stanisor et al., 2013). Furthermore the basal ganglia play an important role in the control of saccades by reward (Hikosaka, 2007; Hikosaka, Takikawa, & Kawagoe, 2000) and pursuit-related signals have been identified recently (Basso, Pokorny, & Liu, 2005; Yoshida & Tanaka, 2009).

5. Conclusions

Our results show that smooth pursuit is sensitive to the salience and the value of moving stimuli. Salience is processed quickly and governs the initiation of pursuit. The first effects of value can be measured 150 ms after pursuit onset, which is close to the end of the open loop phase of pursuit (Lisberger & Westbrook, 1985; Rasche & Gegenfurtner, 2009). This delay is longer than for saccadic eye movements (Schütz, Trommershäuser, & Gegenfurtner, 2012) and smooth pursuit takes also more time to fully converge to the rewarded direction. While saccades are too short in duration to be affected by visual feedback, ongoing smooth pursuit can be adjusted based on its visual consequences. One interpretation of the slow time course of smooth pursuit is that visual feedback is necessary to steer pursuit towards the rewarded motion direction. Additionally the transition to the rewarded direction can be delayed by the difficulty to segment the two motion directions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.08.009.

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